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ON THE QUANTITY AND DYNAMICS OF ANIMAL TISSUES.

BY J. LAWTON WILLIAMS.

EVERY ONE knows that the animal tissues are not fixed and unvarying quantities. From the time of an animal's first appearance in the outer world to that of its disappearance by the natural processes of dissolution it exhibits many morphological changes, so obtrusive as not to require comment. They are spoken of as developmental changes, and are often so radical and thoroughgoing that the later forms in the series bear no resemblance to their antecedent forms. Such are the total metamorphoses of certain insects, crustaceans, worms, and sponges. Partial metamorphoses are gone through even by the highest types, so that the adult form often possesses morphological characteristics which are not present in the young, or *vice versa.* But there are other less obvious changes which affect the tissues, and are not so easily studied by direct observation. Such are the changes in quantity arising from varying rates of nutrition and other disturbing causes. Besides these fluctuations, which are directly referable to immediate causes, there are others which appear to be constitutional, and proceed along definite paths of development throughout the lifetime of the animal. Moreover, these less apparent changes seem to adhere to animal species with much the same persistency that the more ostensible outward differences do. That is to say, just as one can distinguish an adult deer from its young by change in the form of its antlers, so, if he were a thorough expert, he could detect equally important changes in its internal parts which might serve as the basis of distinctions just as important as the ones here employed. In the absence of any extended investigations, it is impossible to speak with quantitative exactness of the inner changes from the time of birth to the attainment of old age. Such a record upon any one animal would be impossible from the very fact that the first investigation would deprive the animal of life. To conduct intelligent experiments on different representatives of the same species would require a knowledge of the age, food, and environments of the different animals dissected, and then we would have to proceed upon a supposition, probably never realized in nature, that all the subjects of the experiment varied together in the quantity and distribution of all their tissues. Obviously such a supposition would be purely artificial; and to insure all the conditions for the faithful execution of the experiment would require precautions so labored and extraordinary as to baffle the most skillful experimenter.

But while it is impossible to obtain exact and absolutely reliable data which may serve as the basis of laws of specific development, yet there are certain general and approximate methods which may lead to very much the same end. Such data may be derived in part by observations of the outward contour as determined by the plumpness or leanness of the animal. It is true that inferences based upon such observations may often be misleading, owing to our ignorance as to just what tissues produce the fullness or shrinkage in any given instance, and as to whether the same amount of shrinkage at different times is caused by the degeneration of the same or different tissues. Many valuable suggestions may be gleaned, however, from post-mortem examinations of typical cases. Such examinations, if found to be often confirmatory of previous conjectures, will tend to inspire confidence in our methods and results. There can be nothing more certain than that most mammals are subject to easily observable changes in their external contour from the time of their birth onward. Puppies and kittens, for example, are clumsy and thick-set when born, the latter being positively corpulent. As growth proceeds, however, the legs and body elongate, and the relative proportions of limbs and body are altered in a marked manner, the body becoming often quite lank. Quite the reverse happens to the calf and colt. They are very gaunt and long-legged, to begin with; but grown cows and horses become decidedly thick and sometimes unwieldy. The muscles also change in form and relative dimensions. Changes like these are points of common remark in the human subject. Plump babyhood and childhood, spare youth, stout manhood, and weazen old age have all found place in familiar proverb and song. All these outward changes are certainly expressions of inner changes equally important and significant.

In early life the vegetative functions preponderate. Eating and attendant growth are the all-important activities. But bye and bye the animal functions of motion come into play. Nutrition then ceases to be the dominant function, and the surfeited tissues give up their useless store to the growing demands of higher activities. The result is a redistribution to suit the specific needs of the animal organization in question. This redistribution does not cease until a new equilibrium is established which harmonizes with the existing orders of activity. Then a stage of equilibrium ensues, which may be called the balance of middle life. It continues until the already abridged functions of nutrition begin to yield further ground, weakened by the approaching exhaustion of an ebbing and dwindling vitality. This waning of the nutritive functions is manifested by a loss of flesh, and the angular, bony framework projects out through the wasted habiliments of muscular and adipose tissue. At last the vital store is exhausted, the nutritive processes cease, and the animal dies. Such, in brief, is the story of the average mammal's life, though the details are often disguised in various ways. While we cannot exactly formulate the variations of tissue at different periods, yet an average of many weighings will not lead us much astray. Such averages of different species closely allied may be compared with profit.

We are all more or less familiar with certain differences of absolute and relative weight and volume in the homologous tissues of different species. Results of this sort, especially on the brains of animals, are quite frequently met with. In all such cases, however, we are often perplexed to know, especially in animals with only remote systematic affinities, just how far it is legitimate to compare apparently homologous organs, and where such comparisons should end. For this reason it is generally well to restrict our comparison to animals of the same subkingdom, and, better still, of the same class, for the greater the divergence of remotely analogous tissues the less reliance can be placed on the comparative results. There are other difficulties which arise in the study of the quantities of tissue in the same animal. In highly organized animals the differentiation of parts is often carried to such extremes, and the histological and anatomical lines of division are so ill defined, that we cannot say precisely where one tissue begins and another ends, and even the distinctions of a tissue as the material endowed with specific physiological functions is necessarily arbitrary and includes heterogeneous elements. To illustrate, it is not uncommon to find tables of the comparative weight of vertebrate brains. The value of such tables from the standpoint of strict homology is not very great. How utterly impossible it would be to find strictly homologous parts in all the cerebral tissues even in the different members of the class Mammalia! Certainly the range of physiological and psychological functions which these tissues discharge in the different members of the class is a very wide one. Some of them are unique and peculiar to one order, and are not represented in the others. Considerations like these bring us to realize that all quantitative studies of the tissues must necessarily proceed upon arbitrary assumption as to what parts are proper subjects of comparison. Probably, after all, the best method of pursuing such studies is to compare tissues with approximately the same physiological functions. This method I have pursued in the case of a few of the higher animals. The weight of the skins, skeleton, muscles, bones, and viscera were made the subjects of comparison. Under the last division were included not only the viscera proper, but also the lungs, brain, and all parts not properly falling under the other divisions. Under the head of skeletal muscles, tendons and ligaments were necessarily included; and under the head of the bones, cartilages and fatty marrows were included. Only a few dissections were made, and hence all inferences based upon them are necessarily incomplete, and require to be stated with extreme caution. The following comparative table gives the results:

Animals.	Skins.	Bodies.	Ratios of Skin to Body (approximate).
Woodchuck,	12 oz.	80 oz.	1 : 7
Rabbit,	3 oz.	23 oz.	1 : 8
Gray squirrel	5 oz.	25 oz.	1 : 5
Black squirrel,	4 oz.	24 oz.	1 : 6
Skunk,	13 oz.	3 lbs. 10 oz.	1 : 4½

Animals.	Muscles.	Bodies.	Ratios of Muscles to Body (approximate).
Woodchuck,	1 lb. 4 oz.	5 lbs.	1 : 4
Rabbit,	10 oz.	23 oz.	1 : 2
Gray squirrel,	12 oz.	25 oz.	1 : 2
Black squirrel,	11 oz.	24 oz.	1 : 2
Skunk,	13 oz.	3 lbs. 10 oz.	1 : 4½

Animals.	Bones.	Bodies.	Ratios of Bones to Body (approximate).
Woodchuck,	1 lb.	5 lbs.	1 : 5
Rabbit,	5 oz.	23 oz.	1 : 4½
Gray squirrel,	4 oz.	25 oz.	1 : 6
Black squirrel,	4 oz.	24 oz.	1 : 6
Skunk,	11 oz.	3 lbs. 10 oz.	1 : 5

Animals.	Viscera.	Bodies.	Ratios of Viscera to Body (approximate).
Woodchuck,	1 lb. 12 oz.	5 lbs.	1 : 3
Rabbit,	5 oz.	23 oz.	1 : 4½
Gray squirrel,	4 oz.	25 oz.	1 : 6
Black squirrel,	5 oz.	24 oz.	1 : 5
Skunk,	14 oz.	3 lbs. 10 oz.	1 : 4

The fact which impresses us most about these figures is that the relative proportions of the tissues here considered are far from constant in the same and in different animals. The right-hand figures in the column of ratios are well calculated to emphasize this fact. The tegumentary, bony, nutrient, and motor tissues do not each have equal weights in the same animal, and the ratio of their weights to the body-weights are not the same in different animals. For example, the ratio of the weights of the skin to the body vary all the way from 1 : 8 in the rabbit to 1 : 4½ in the skunk; the ratios of the muscles from 1 : 2 in the rabbit and squirrels to 1 : 4½ in the skunk; the ratios of bones from 1 : 4½ in the rabbit to 1 : 6 in the squirrels; and the ratios of the viscera from 1 : 3 in the woodchuck to 1 : 6 in the gray squirrel. Thus it appears that variations of one-half are not uncommon for the same tissue in different animals, and much profounder differences exist in the weights of different tissues of the same animal. Without doubt, more extensive dissections would reveal even greater extremes in the quantities of tissue in other mammals and in vertebrates generally. Certainly the nerves and the brain exhibit immense quantitative differences in animals of different species. While the brain of the elephant, the largest of terrestrial mammals, has the greatest absolute weight, and that of the whale, the largest of all mammals, the next in size, yet among the smaller animals it is well known that the brain of man is preëminent in size. The brains of fishes and reptiles are exceedingly small in proportion to the size of the body, and the brain of Coryphodon, the prototype of the Ungulata, from the early Tertiary, was relatively much less than the average existing mammalian brain. The several tissues differ immensely in the range of their quantitative variations. Some of them, as the bones and muscles, grow under mutual limitations prescribed by the mechanical conditions of animal movement. If the animal is to move it must have motor tissues, and it must have hard parts upon which the motor tissues can act. The existence of the one necessitates the existence of the other, and that in certain quantity as well. The quantity of the one is reactionary upon the quantity of the other. If one is destroyed the other no longer has any use, and eventually suffers degeneration. Like relations subsist between certain correlated organs of the viscera. They act and react upon one another, and hence their growth and decline must go on together. There are other tissues the growth of which is mutually antagonistic. Darwin and Cope have cited the examples of the Artiodactyla where the evolution of the antlers is accompanied by a disappearance of some of the teeth. Facts of like import are not wanting in the case of the other tissues. Cope explains them by assuming that the animal has a fixed complement of vitality or bathmic force, and hence, by the principle of the conservation of energy, an expenditure in one form of growth must be compensated for by an equivalent suppression of some other form of growth. Cephalization is really a special case of this general principle, where the lines of maximum growth converge in a common direction. The acceleration of parts headward is coincident with the abortion of parts tailward. Under this view it is easy to suppose that the disappearance of the tail in man was accomplished by an enlargement of his cranial capacity, and the vital energy that was expended in its movement has now been transformed into some higher psychical energy. Finally, there are some other tissues the quantity of which does not seem to be subject to the limitative adjustments of other tissues, because they are not directly concerned in the vital economy, and they fluctuate very perceptibly with the changing conditions of the animal's environment. Such is the adipose tissue. Cells of fat may increase independently of any mechanical laws prescribed by other tissues (of course within limits compatible with life), as in the omentum of corpulent people and the layers of adipose tissue in swine. We thus see that there are quite well-defined types of growth among the tissues of animals. There are those which increase and decrease together, those which increase at the expense of others, and those which vary independently. Of course these lines are not absolutely distinct, and probably every tissue in some degree embodies them all. This classification is given as having a general value only; but while there are specific and individual variations which have no apparent connection with any general evolutionary principles, there are variations, extending over longer periods of time, which have a historical value to the anatomist and paleontologist. They are the larger cycles of change in which these individual cycles move and exist. In the brief period of a human lifetime they are disguised by the seemingly irrelevant fluctations of the present, and it is only in the light of a remoter history that we gain a full conspectus of the progress of these events.

All through the Paleozoic and Mesozoic ages there was a remarkable profusion of molluscan and radiate life. Lime-secreting animals were the prevailing type in all seas, and the seas were everywhere. In many places the rocks are almost entirely composed of the remains of these animals. Finally fishes made their appearance. They continued to develop, and have reached their highest phase of specialization at the present time. Then the reptiles came, and at length the mammals. This succession has been marked by a concomitant succession in the relative quantities of animal tissues. When the primeval seas were surcharged with carbonate of lime the organisms then living rapidly used up the excess in secreting protective coverings for their softer parts. In some of the early

Brachiopoda, as Discina and Productus, a calcareous shell made up a large part of their weight. The rugose and tabulate corals, the Cephalopods, and many other forms were permeated through and through with walls and tables of calcareous masonry. This process continued for a long succession of ages. Even when the early fishes appeared they too were plated and shielded by thick secretions of carbonate of lime. But as the type of fishes expanded a new tendency became developed, which has continued to manifest itself ever since. Even the early Ganoids possessed a much greater quantity of soft tissue in proportion to the hard parts than did the Brachiopods and corals. This, of course, was an indispensable prerequisite to the free and roving life which they led. Had they been weighted as heavily as some of the Brachiopods, locomotion would have been out of the question; in fact, it may be enunciated as a general principle that wherever an animal is found capable of vigorous and long-continued locomotion, there we may be sure to find the motile elements of the body sustaining a high ratio to the inert elements. But later on forms like the Cestracionts and other sharks must have had a very large excess of soft parts over hard parts. Later still the heavy ganoid scales were discarded for the lighter ones of the Teleosts. The secretions of lime became less, and the excess of hard parts over soft parts was diminished until the opposite relation existed. While this tendency may not be traceable in all cases, yet there are a sufficient number of instances to warrant the generalization that the development of animal life has been marked by a growing diminution in the quantity of hard parts, and a relative increase in the quantity of soft parts. The gigantic reptiles of the Cretaceous age and mammalian life of later times all point to this conclusion. The change in the relative quantities of hard and soft parts was attended by other correlated changes. As the soft parts were liberated from the incubus of the hard parts they gradually differentiated in various directions, to suit the altered conditions of their environment. By reducing its calcareous integument the animal was more exposed to the attacks of its enemies; and this exposure necessitated one of two things,—either it must take on protective colors or spines, or it must differentiate motor tissues and organs by which to escape those enemies. In some cases both lines of development have been pursued in some part by the same animal. The locomotive function must certainly have played a highly important part in the life of fishes from the very first, and in birds its manifestations are even more intense. But with the evolution of locomotive powers there arose a need of a system of external or internal leverage, and the result of that necessity is the exoskeleton and endoskeleton of the Arthropoda and Vertebrata respectively. A nutritive apparatus necessarily coëxisted with the lime-secreting activity. But when the factor of locomotion became added to the animal life new differentiations of structure were called into being. Function and tissue reacted again and again in endless combinations, and the present diversities of organic structure were the result. That result was marked not only by qualitative but quantitative peculiarities, and it is these peculiarities that we have been discussing. Such, in brief, is the historical outline.

We now pass on to consider the dynamics of the subject. It is a patent fact that a division of labor is beneficial to all the laboring elements. It is no less true that it results in some degree of dependence between those elements. The degree of the dependence is heightened the farther the specialization is carried. This is eminently true of the animal orgamsm. In its simplest expressions as *Protamœba* an absolute independence between the parts everywhere prevails. All parts alike respond to all stimuli, and no part is anything in particular, but everything in general. In higher forms the structures are more diversified, and they assert their individuality by differential responses to external stimuli. Moreover, each member gives a complete response only when it sustains a connection with all its fellow-members. The several members form a joint society, whose union is strength and whose dissolution is ruin. Such is the polity of the animal body. Now we have seen that the several tissues vary in quantity. They vary in the same individual at different periods of life, and in individuals of equal age in the same and in different species. Such variations in the tissues must profoundly affect the amount of functional activity. Suppose we compare two of the animals given in the tables, the woodchuck and the rabbit. The ratios of the weight of muscle to the weight of body in the two animals stand in the proportion of 1 : 2. That is to say, the rabbit has two pounds of muscle for every one possessed by the woodchuck, which it can use in moving its body. Now the specific energy of striped muscle in animals as widely separated as the bird and man stand only in the insignificant ratio of 1200: 1087 ("Animal Mechanism," E. J. Marey), so that we do not feel that we are assuming too great impossibilities when we call the specific muscular energies of the woodchuck and rabbit equal. Now this equality can only subsist for a period of extended duration on condition of equal metabolic activities in the two tissues. These activities, in turn, will depend on the food supply, digestion, and all the preliminary acts of nutrition. But to avoid complications we will adhere to our first assumption. Now the woodchuck has to move twice the inert mass in proportion to its muscular weight as the rabbit. To do this it can execute only one-half the quantity of motion as the rabbit. Then the rabbit leads a life twice as active as the woodchuck. But the viscera of the woodchuck are to those of the rabbit nearly as 3 : 2, and assuming equal nutritive powers in equal weights of the viscera, the difference of muscle weight would be partially offset by a canceling difference in the rates of repair of the wasting tissues. This assumption, however, that equal quantities of viscera repair equal amounts of waste, is not a safe one. Besides, it will be remembered that in these experiments organs as widely diverse in function as the brain, lungs, liver, and heart were, to avoid confusing details, weighed together and classed as viscera.

The rate of assimilation and repair of the muscles would clearly depend upon the size and activity per unit quantity of the organs concerned in the vegetative functions. Organs of different function, as the brain (which is extremely variable in size), would vitiate the comparison between equal quantities of viscera as here employed. But, what is still more adverse to the assumption, there is no good reason for supposing that equal quantities of organs discharging the same functions create equal functional products. Butchers say that in old cows the intestines have a much greater size in proportion to the body than in young cows and heifers. They are also poorer, and it requires a much greater amount of food to produce a given amount of flesh than in younger animals. This case seems to indicate that the efficiency of the organ degenerates with increasing size. Of course this is not always true, and there are marked instances to the contrary, as in the relatively large brains of certain intellectual prodigies and the heavy biceps of professional pugilists. Probably the differences of size in the functional organs of the viscera are, in many cases, due to the growth of indifferent tissues as fat and connective fibers. Perhaps their presence in the case of the cows already mentioned may even impede the normal discharge of the functions. Be this as it may, it is undeniable that the greater quantities of viscera are by so much an added incubus to the movements of the animal. It is, of course, self-evident that in most cases all the tissues not directly concerned in the contractions which produce motion are in some degree adversative to such contractions. Only a few of the voluntary muscles are used in any one movement, and all the rest of the body is, for the time being, a dead weight to be overcome; so that in the simplest of our daily movements the active and passive parts are continually shifting about, and the waves of maximum activity travel now here and now there. All the tissues, save the voluntary muscles, are perpetually inert relative to movements in the environment. They are at one time impelled to passive movements, and at another time are quiescent, according to the character of the movement. They are in one sense a necessary evil, impeding and yet indirectly promoting the movements of the animal.

Lastly, we have to consider the bones. Without doubt they are inert elements. Yet that very inertness serves a useful purpose in the animal movements. If we compare the ratios of the bones to the body and of the muscles to the body in the woodchuck and rabbit, we are surprised at the absence of parallelism which a knowledge of their mutual connection would lead us to expect. While the muscles of the woodchuck are to those of the rabbit relative to the body as 1 : 2, the bones are nearly equal in the same comparison. This is explained by the fact that the total weight of body to be supported is greater in the woodchuck, and since the quantity of muscle is relatively smaller, the animal is forced to a sedentary life and does not move about much. Even the forms of body in the two animals harmonize with this view. The woodchuck is stout and heavy, the rabbit is agile and slender. Just as the heavy bones of the woodchuck are indicative of its sluggish habits, so the light bones of the rabbit point to an opposite inference. Very much more could be said of the quantities and dynamical values of the animal tissues, but this must suffice at present. It is hoped that further evidence will be brought forward on some of the points here barely alluded to. The subject is certainly a very fruitful one for future research.